

Growth of Three Species of Abalones (*Haliotis*) in Southern California

by

THEODORE C. TUTSCHULTE AND JOSEPH H. CONNELL¹

Department of Biological Sciences, University of California,
Santa Barbara, California 93106, U.S.A.

Abstract. Growth of tagged juvenile pink abalones (*Haliotis corrugata*) in the field and laboratory ranged from 11 to 16 mm per yr; adult annual growth ranged from 4 to 8 mm. Adults transplanted from shallow water to near their lower depth limit grew hardly at all. Juvenile green abalones (*H. fulgens*) tagged in the field and laboratory grew from 13 to 16 mm per yr; adult annual growth ranged from 4 to 7 mm. Transplants to depths below the normal limit did not grow. For white abalones (*H. sorenseni*) in the laboratory, juveniles grew 25 mm per yr, adults grew 10 mm per yr. In the field adults showed little shell growth, probably because they actively eroded their shells on the experimental tiles to which they had been transplanted. In all species smaller individuals grew faster in absolute length than did larger ones, independent of treatment. Growth rates calculated from polymodal size frequency analyses agreed closely with those from direct observations of tagged individuals. Based on these data, von Bertalanffy growth curves were constructed. Relative growth in soft-body weight decreased gradually with increasing size. All three species showed seasonal variations in growth; each species had a different season of maximum growth. During the autumn when gonad growth occurs in adult pink abalones, growth was significantly lower than in the preceding summer or the following winter. Juvenile pink abalones did not show this pattern. These results suggest that there may be a shift in energy allocation into reproduction and away from growth in this species. Adult pinks and greens would eventually reach a maximum size in about 50 yr; whites would do so in about 34 yr.

INTRODUCTION

This study was undertaken as part of a comparative investigation of three species of abalones, *Haliotis fulgens* Philippi, *H. corrugata* Wood, and *H. sorenseni* Bartsch, referred to here as the green, pink, and white abalones respectively, in southern California. Growth rates are important indicators of well-being in a population and are also useful in estimating age when no other direct method, such as annual rings, is available. We have measured variations in growth rates under different environmental conditions and in different seasons for the three species and have compared these to the growth of other species elsewhere. We have also fitted mathematical models of growth with age to make predictions for older ages where data are scarce.

AREA AND METHODS

All collections were made between April 1969 and April 1973 in the Isthmus region of Santa Catalina Island within an 800-m radius of the coordinates 33°27'N, 118°29'W.

The depths and frequency of collections are described in more detail below. This area faces the mainland across the 32-km-wide San Pedro Channel and thus is protected from westerly and southwesterly oceanic swells and the occasional southeasterly storms occurring in this region, but is exposed to wind and waves from the northwest, north, and northeast. Except for periods of northwest storms, there is very little wave action, but the area is regularly swept by strong tidal currents that sometimes reach a speed of 3 knots. There are dense beds of giant kelp (*Macrocystis pyrifera* (Linnaeus) C. A. Agardh) along the shore and on offshore reefs. These beds extend from approximately 2 to 20 m below MLLW. A dense understory beneath the *Macrocystis* canopy is comprised of a variety of red and brown algae. Between the 20- and 40-m-depth levels, the large leaf kelps *Laminaria farlowii* Setchell and *Agarum fimbriatum* Harvey are the dominant algal forms.

Direct Observations of Marked Individuals

We followed the growth of individual abalones (1) under laboratory conditions, (2) in cages on the sea floor, and

¹ Reprint requests should be sent to the second author.

(3) marked, released in the wild, and then recaptured. For these studies, each animal was marked with a numbered stainless steel tag attached to the shell by means of a stainless steel wire looped through two adjacent respiratory pores, similar to CROFTS (1929). A notch was filed in the shell margin in such a way that a small triangular area of nacre would remain exposed on the outer shell surface following shell growth (LEIGHTON, 1968), thus assuring that growth could still be measured in the event of loss of the tag. Growth was measured as the increment to anterior-posterior shell length. Weight-length relationships were determined for each species from large series of animals collected and killed for reproductive studies (TUTSCHULTE & CONNELL, 1981).

In the laboratory, animals were held in running, aerated, ambient seawater at the University of California, Santa Barbara, with food (blades of *Macrocystis pyrifera*) always present. Each animal was remeasured at intervals for one or more years. In the field, three different types of experiments were done. In the first, animals held in cages on the sea floor were provided with refuges consisting of 30 × 15 × 2.5-cm clay roofing tiles stacked with 2.5-cm spacers between them. Each rack of tiles was enclosed in a cage constructed of neoprene mesh having square openings 8 mm on a side. Food, consisting of the various brown and red algae in approximately the same proportions as encountered by the abalones in nature (TUTSCHULTE & CONNELL, in press), was put into each cage at monthly intervals and in sufficient quantity that some algae remained at the end of each interval between feedings. The cages were placed at depths of 2 and 9 m. The animals were remeasured at 3- to 4-month intervals over periods of up to 13 months. In this series, new animals suitably tagged were added between intervals to replace abalones that had died. The second field series consisted of releasing marked pink and green abalones at 5 m depth on natural substrates from which all abalones had been removed; survivors were remeasured after 1 yr. In the third field series, abalones whose shell margins had been notched, but which were not individually tagged, were released onto a pile of roofing tiles at 9 and at 20 m. The tiles had been arranged on the sea floor several months before the abalones were released onto them and thus had been leached and had accumulated a growth of benthic diatoms and attached algae, which provided food for the smaller abalones.

Growth Estimates from Analyses of Size-Frequency Data

A method of estimating growth from an analysis of polymodal size-frequency distributions using probability paper (HARDING, 1949; CASSIE, 1950, 1954) was used to extract year classes from population samples taken at intervals over a 2-yr period. This method dissects the observed polymodal curves into a series of overlapping normal curves. Information on spawning times (TUTSCHULTE

& CONNELL, 1981) was used to estimate the age of each mode. For example, since the greens have a single spawning season in July–August each year, the age of each mode of a sample taken in April was estimated to be a year class plus 0.75 yr. Thus, the zero-year class in that sample was estimated to be 9 months old, the one-year class to be 21 months old, and so on. Calculated growth rates for comparison to those directly observed were derived from a linear regression of mean shell lengths of year classes on estimated ages for the first 4 yr for pinks and first 6 yr for greens and whites.

The use of length-frequency analysis allows us to link growth to age, using the fitted growth curves described below. However, it is necessarily a less direct method for estimating growth than observations of marked individuals. Therefore, we used it only after comparing its results to those from the direct observations. The two methods gave very similar results (Table 1).

While many workers have applied the probability paper method used here (HARDING, 1949; CASSIE, 1950, 1954; NEWMAN, 1968; POORE, 1972; TUTSCHULTE, 1976; SAINSBURY, 1982), other statistical methods have also been developed to separate year classes in length-frequency data (e.g., HASSELBLAD, 1966; YONG & SKILLMAN, 1975; MCNEW & SUMMERFELT, 1978; MACDONALD & PITCHER, 1979; SCHNUTE & FOURNIER, 1980; FOURNIER & BREEN, 1983; SHEPHERD & HEARN, 1983). In one instance (SAINSBURY, 1982) the probability paper method of CASSIE (1950) was compared to the statistical method of YONG & SKILLMAN (1975), using data from an abalone in New Zealand. In 13 of 15 comparisons of the mean length of a particular age class, the estimates of the two methods differed by less than 8%. Thus, the two methods gave quite similar estimates of size at a given age for an abalone. The closeness of this comparison, and the similarity of the growth rates from our direct observations to those calculated by the probability paper method, lend confidence to this method.

Fitted Growth Curves

To describe the growth of abalones mathematically, we used growth models developed for fish populations (RICKER, 1975). Early work by BRODY (1927) described the increase in length of domestic animals as an S-shaped growth curve, with the early growth stanzas having an increasing slope over time and the later ones having a decreasing slope. Since our growth measurements were mainly on animals older than about 0.3 yr, we have assumed, as in most work on growth of fish and invertebrates, that this growth is best described by a curve of decreasing slope.

We have used two different growth models. The first was proposed by VON BERTALANFFY (1934, 1938, 1960). FABENS (1965) has derived the following simplified equation for the von Bertalanffy growth curve for length vs. age:

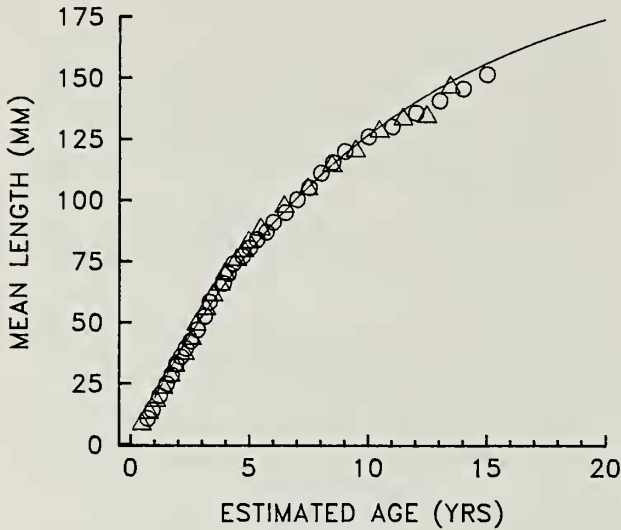


Figure 1

Growth of pink abalones (*Haliotis corrugata*). The points shown as \circ and Δ were derived from analyses of polymodal size frequencies from pooled samples taken in 1971 and 1972, $n = 509$ and 685, respectively. The continuous curve was calculated from a von Bertalanffy equation, with $K = 0.097$ and asymptotic size of 202 mm (see text).

$$L = L_{\infty}(1 - be^{-Kt}). \quad (1)$$

This is a curve of the decaying exponential type in which the animal reaches half of the difference between length at birth (equivalent to the size at which they settle on the substrate from the plankton), L_0 , and the asymptotic maximum length, L_{∞} , at age $t = \ln 2/K$. Because the von Bertalanffy growth equation fits the growth data of a wide variety of animals (e.g., fish, mammals, and many invertebrates, including some prosobranch mollusks) and because "... the underlying concepts are ... the most satisfactory of those which have so far been put forward ..." (BEVERTON & HOLT, 1957), the model has gained rather wide acceptance among biologists, at least for descriptive purposes, and has been incorporated into methods devised for estimating individual growth rates and population mortality rates from size data for fish or various invertebrates (e.g., BEVERTON, 1954; FABENS, 1965; GREEN, 1970; EBERT, 1973, 1975, 1980; SCHNUTE & FOURNIER, 1980), including abalones (e.g., FORSTER, 1967; NEWMAN, 1968; POORE, 1972; TUTSCHULTE, 1976; HAYASHI, 1980; SAINSBURY, 1982; SHEPHERD & HEARN, 1983; FOURNIER & BREEN, 1983).

The von Bertalanffy curves for each species in Figures 1-3 were obtained by setting L_{∞} of equation (1) equal to the maximum size that we have observed for each species and L_0 equal to 1.0 mm at age 0.1 yr (LEIGHTON, 1972, found that white abalones reached 0.7 mm at 0.1 yr in the laboratory). The value for t at length $(L_{\infty} + L_0)/2$ was determined from the data in Figures 1-3, which were obtained from size-frequency data as described above (see

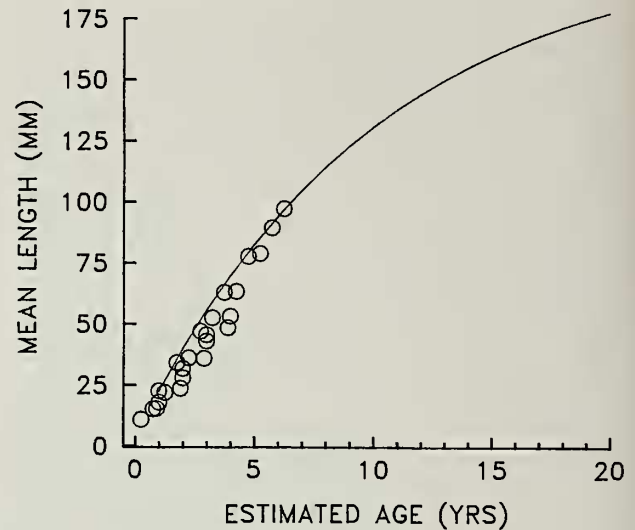


Figure 2

Growth of green abalones (*Haliotis fulgens*). The points were determined from analyses of polymodal size frequencies from pooled samples taken in 1970 to 1972, $n = 444$. The continuous curve was calculated from a von Bertalanffy equation, with $K = 0.101$ and asymptotic size of 205 mm (see text).

TUTSCHULTE, 1976, for details). This t value was then used in the model relationship $t = \ln 2/K$ at length $(L_{\infty} + L_0)/2$ to calculate K (FABENS, 1965). The third parameter b becomes eliminated by algebraic manipulation as shown by FABENS (1965).

A second mathematical equation of the decaying exponential type was used to calculate growth coefficients and asymptotic sizes from data on direct observations of marked individuals. FORD (1933) (see also WALFORD, 1946) developed the expression:

$$L_{t+1} = L_{\infty}(1 - k) + kL_t \quad (2)$$

where the growth coefficient $k = e^{-K}$, in which K is the von Bertalanffy coefficient in equation (1). This equation expresses a type of growth in which the increment in each year is less than that in the previous year by the fraction $(1 - k)$ of the latter (RICKER, 1975). If L_{t+1} is regressed against L_t , k is the slope of the line and the intercept is $L_{\infty}(1 - k)$, from which L_{∞} can be calculated. These regressions were calculated from direct measurements of marked individuals, with L_t being the initial length and L_{t+1} being the length after 1 yr.

The von Bertalanffy equation (1) can be used to predict the age at any future size. From it FABENS (1965) derived the following equation (his equation 4.1):

$$L_{t+\Delta t} = L_t + (L_{\infty} - L_t)(1 - e^{-K\Delta t}). \quad (3)$$

Rearranging and solving for Δt :

$$\Delta t = \ln[1 - (L_{t+\Delta t} - L_t)/(L_{\infty} - L_t)] / -K. \quad (4)$$

We used equation (4) to calculate the average age at which

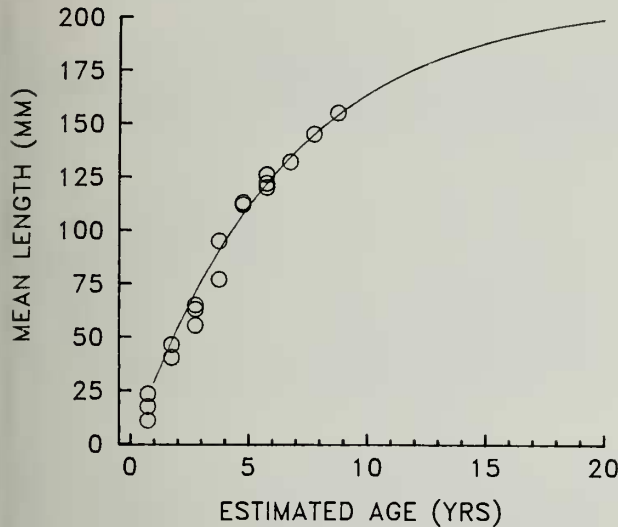


Figure 3

Growth of white abalones (*Haliotis sorenseni*). The points indicate the individual values from Table 4. The continuous curve was calculated from a von Bertalanffy equation, with $K = 0.154$ and asymptotic size of 210 mm (see text).

an abalone would grow to within 1 mm of its asymptotic size.

RESULTS

Annual Growth of Marked Individuals

Laboratory growth: Increments of shell lengths of pink, green, and white abalones held in the laboratory are given in Table 1. These growth rates show the same pattern evident in the rates obtained by the other three methods: small whites grow about twice as fast as small pinks and greens, the latter two species appearing to grow at quite similar rates.

Growth in the field: The average growth rate of the group of pinks <100 mm initial length released on tiles at 9 m depth was about $\frac{1}{3}$ higher than that of those held in cages nearby at the same depth (Table 1). Of a large group of tagged juvenile pinks released at 5 m depth in a 20-m² area of natural substrate from which all abalones had been previously removed, 16 survivors were recovered over a year later. This group grew in the wild at about the same rate as the uncaged pinks on the tiles (Table 1). Although only 10 green abalones smaller than 100 mm survived to be measured after a year on the seabed, their growth rates were about the same whether they were in cages, on tiles, or released on natural substrate, and all were similar to the rates in the laboratory (Table 1).

Larger pinks, greens, and whites grew slower than smaller ones in all treatments (Table 2). (Complete data on growth of each individual, with graphs of growth increment vs. initial size for each treatment, are given in TUTSCHULTE, 1976.) The only instance in which this relationship differed among treatments was with white abalones (Table 2), owing to the fact that, in the field, only large individuals were observed. The values of the growth coefficients and asymptotic sizes, calculated with equation (2) from the data on observations of marked individuals, are given in Table 3.

Growth Rates Derived from Size-Frequency Data

The analyses of polymodal size frequencies of collections of pink abalones in the summers of 1971 and 1972 yielded the results shown in Figure 1. Because these two pooled samples were very large, we were able to use this method for size frequencies up to approximately 150 mm. Analyses of two larger samples ($n = 1881$ and $n = 1822$) from the pink population at Santa Cruz Island taken in March 1975 yielded very similar results (TUTSCHULTE, 1976, ap-

Table 1

Annual growth rates expressed as shell length increment in mm of small and large abalones (pinks, *Haliotis corrugata*; greens, *H. fulgens*; whites, *H. sorenseni*). Values are mean/SD (n).

Treatment	Pinks: initial length (mm)		Greens: initial length (mm)		Whites: initial length (mm)	
	<100	≥100	<100	≥100	<100	≥100
1. Held in laboratory	11.5/6.5 (175)	8.0/6.6 (13)	13.6/6.0 (24)	—	25.1/11.7 (10)	9.9/6.6 (9)
2. On tiles on the seabed at 9 m depth	14.8/3.6 (7)	3.9/2.9 (26)	13.6/2.9 (3)	4.0/2.4 (15)	—	1.7/1.8 (17)
3. On tiles on the seabed at 20 m depth	—	0.5/0.8 (35)	—	0.1/0.3 (19)	—	1.3/1.7 (15)
4. Caged on seabed at 9 m depth	11.7/4.8 (25)	—	13.0/7.7 (5)	7.0 (1)	—	—
5. Marked, released in wild for 1 yr at 5 m depth	16.4/7.1 (16)	—	13.0/9.2 (2)	—	—	—
6. Derived from size frequencies	16.4	—	16.0	—	23.3	—

Details of dates and initial sizes given in TUTSCHULTE, 1976.

Table 2

Growth increment vs. initial size; tests of whether the slopes of regressions were significant and equal among the treatments given in Table 1.

A. Pink abalones				
1) Analysis of covariance				
Source	df	Mean square	F	P
Initial size	1	2334.25	68.27	0.0001
Treatment	3	58.19	1.70	0.17
Size × treatment	3	77.95	2.28	0.08
Error	254	34.19		

2) Mean values

Treatment	Depth (m)	Mean annual growth increment (mm)	Mean initial size
1. Laboratory	—	11.27	55.4
2. Tiles on seabed	9	6.36	109.6
4. Caged on seabed	9	11.72	39.2
5. Released in wild	5	16.44	31.8

B. Green abalones*

1) Analysis of covariance

Source	df	Mean square	F	P
Initial size	1	1047.82	48.89	0.0001
Treatment	2	27.38	1.28	0.29
Size × treatment	2	53.89	2.51	0.09
Error	41	21.43		

2) Mean values

Treatment	Depth (m)	Mean annual growth increment (mm)	Mean initial size
1. Laboratory	—	13.5	53.8
2. Tiles on seabed	9	5.6	113.8
4. Caged on seabed	9	13.0	33.3

C. White abalones

1) Analysis of covariance

Source	df	Mean square	F	P
Initial size	1	2301.29	35.14	0.0001
Treatment	1	630.48	9.63	0.0040
Size × treatment	1	63.25	0.97	0.3331
Error	32	65.49		

Table 2

Continued.

2) Mean values

Treatment	Depth (m)	Mean annual growth increment (mm)	Mean initial size
1. Laboratory	—	17.89	85.79
3. Tiles on seabed	9	1.67	135.77

* For green abalones, the treatment "released in wild" had only two individuals, so was not included in this analysis.

pendix fig. 1). Both samples show that up to about 70 mm shell length (age 4 yr), growth rate is approximately linear at 16.4 mm/yr, but declines progressively thereafter. A von Bertalanffy curve was fitted for growth of pinks (Figure 1). The growth coefficient and asymptotic sizes are given in Table 3. As can be seen, they are similar to those calculated from equation (2) with the exception of the one based on individuals from the sea floor, which had a smaller asymptotic size.

The results of the polymodal frequency analyses of the green population samples are given in Figure 2. These data suggest that growth in length of green abalones is approximately linear over the first 6 yr at a rate of about 16.0 mm/yr. These samples were too small to use a polymodal analysis for sizes above 100 mm. Therefore, since the growth of pink abalones appears to be closely approximated by a von Bertalanffy curve after they reach sexual maturity (Figure 1), we have assumed the growth of green abalones follows the same pattern and have fitted a von Bertalanffy curve for growth (Figure 2). The growth coefficient and asymptotic size are given in Table 3; they agree well with those calculated from direct observations of marked individuals.

For white abalones, large samples are difficult to obtain since the population lives at greater depths than the other species. Because data on this species are scarce, we present an analysis of two small samples collected during search dives at a depth of 33 m in late November of 1971 and 1972. All spawning in the white population at Santa Catalina Island occurred in one short period, in March for the three preceding years (TUTSCHULTE & CONNELL, 1981). Assuming that average annual growth rates do not vary among years, we grouped the size data as shown in Table 4. If the mean values of each group are plotted against the age estimates we have attributed to them, the results are consistent with a linear growth rate for the first 5 yr that is nearly double those of pinks and greens and very similar to the rate observed for whites in the laboratory (Table 1). The limited data indicate that older whites grow slower. A von Bertalanffy curve was fitted for growth (Figure 3).

Table 3

Calculated values of growth coefficients, asymptotic sizes, and age at 1 mm less than the asymptotic size, for three species of abalones. The laboratory and sea-floor data are from direct observations of marked individuals.

Species	Source of data	von Bertalanffy growth coefficient		Asymptotic size (L_{∞} - 1.0 mm) L_{∞} (mm)	Age at 1.0 mm yr
		n	K		
A. Ford model (equation 2)					
Pinks	Laboratory	188	0.080	201	57.6
Pinks	Sea floor, 5 & 9 m	74	0.109	169	40.7
Pinks	Size frequencies, 1971	15	0.090	185	50.3
Pinks	Size frequencies, 1972	14	0.089	184	50.8
Greens	Sea floor	26	0.092	179	48.8
Whites	Laboratory	19	0.142	221	33.1
B. von Bertalanffy model (equation 1)*					
Pinks	Size frequencies, 1971	509	0.097	202	54.5
Pinks	Size frequencies, 1972	685	0.098	202	54.1
Greens	Size frequencies, 1970-1972	24	0.101	205	52.9
Whites	Size frequencies, 1971-1972	13	0.152	210	35.0

* For the von Bertalanffy model, asymptotic size was taken as the largest individual found.

The growth coefficient and asymptotic size are given in Table 3; they agree well with those calculated from direct observations of marked individuals. From the different sets of data, the average ages at which these abalones would reach lengths within 1 mm of maximum were calculated, using equation (4). They are about 34 yr for whites and about 50 yr for pinks and greens (Table 3).

Variations in Growth Rates by Season

Average growth rates for periods of about 3 months for pinks caged at 9 m depth varied by a factor of four, with the highest value in spring and early summer (April to July) followed by the lowest rate in late summer and autumn (July to November), as shown in Tables 5 and 6. Lower rates were also shown in the other seasons by both this group and a second group of pinks at 2 m. Green abalones in the cages at 9 m depth showed seasonal average growth rates that varied six-fold, from a low value in the late winter (January to April) to a high rate in the late summer/autumn (July to October). The group of greens held at 2 m depth grew at about the same rate as those caged at 9 m in the same season. All seasonal variations were statistically significant (Table 6).

In the laboratory, similar patterns of seasonal variations in growth rates were shown by pinks (faster in spring-summer, slower in autumn-winter), but greens grew fastest in winter-spring and slowest in summer (Table 7). Whites held in the laboratory also exhibited a seasonal growth pattern, most rapid in winter-spring and slowest in autumn. Thus, each species had a different season of maximum growth: pinks in spring to early summer, greens in late summer to winter, and whites in spring.

To test the hypothesis that a shift in energy allocation into reproduction causes a reduction in growth, the growth

rate during the season of most rapid gonad enlargement was compared to that in the preceding and following seasons. If the hypothesis is correct, growth of adults should be significantly less in the reproductive season than in the other seasons. Juveniles, on the other hand, should not show this pattern. Sufficient data exist only for pink abalones in the laboratory; pinks mature at 40 to 50 mm length, and gonads enlarge in the autumn (TUTSCHULTE & CONNELL, 1981). Table 7 shows that growth in individual adult pink abalones was significantly less in autumn than in the preceding summer or the following winter. Juvenile growth decreased between summer and autumn but did not increase the next winter. These data are consistent with the hypothesis of a shift in energy allocation from growth into reproduction during the season of rapid gonad enlargement in adult pink abalones.

Variations of Growth with Depth

Pinks and greens in shallow water (less than 10 m depth) appear to grow at about the same average annual rates (Table 1). In an experiment in which large greens and pinks collected from a 5- to 7-m depth band were transplanted to an artificial habitat at 20 m, the pinks grew slowly at this much greater depth, while the greens did not grow at all (Table 1). In fact, the few greens that survived this transplant for 4 yr lost more than one-half of their body weight over a 2-yr period (TUTSCHULTE, 1976). This is probably related to the lower temperatures and the decreased abundance of food at greater depths (TUTSCHULTE & CONNELL, in press).

Large whites transplanted to artificial substrates at 9 m grew much slower than pinks and greens of similar size; some actually decreased in length (Table 1). Yet whites brought into the laboratory (equivalent in some respects

Table 4

Growth rates of white abalones from size frequencies (mm) grouped by eye. Collections from 33 m depth, November 1971 and November 1972.

Year class	Estimated age (yr)*	Observed shell length	Mean/SD shell length of class	Estimated annual growth rate
0	0.7	11.0 17.5 23.5	17.3/6.3	23.1†
1	1.7	40.5 46.5	43.5/4.2	26.2
2	2.7	55.5 63.0 63.0 65.0	61.6/4.2	18.1
3	3.7	77.0 81.0 95.0 96.0	87.3/9.7	25.7
4	4.7	112.0 113.0 114.0	113.0/1.0	25.7
5	5.7	120.0 122.0 126.0 126.0	123.5/3.0	10.5
6	6.7	132.0	—	8.5
7	7.7	145.0	—	13.0
8	8.7	155.0	—	10.0

* The white population in the Isthmus area of Santa Catalina Island spawned only in March during each of the four years of this study, 1970–1973 (TUTSCHULTE & CONNELL, 1981). Hence, whites of the zero-year age class were assumed to be 0.7 yr old in November, those of the 1-yr age class were assumed to be 1.7 yr old and so on.

† The annual rate for the zero-year class was calculated by assuming the growth rate was linear in the first year and adding 33% to the calculated mean length of the 0.7 yr old group.

to being transplanted to the shallow subtidal zone) grew much faster than pinks and greens under the same conditions. Whites placed on tiles at their natural depth of 20 m also grew very slowly. We offer the following explanation for this apparent anomaly.

The shell of an abalone is elongated along the anterior-posterior axis and most of the shell enlargement takes place by adding to the anterior end and to a lesser extent to the right side (see POORE, 1972, for detailed description). If this process takes place on a convex surface (the substrate where many large white abalones live), the margin of the shell aperture will not lie in a plane, as the margin of an oval platter does. When such a shell is placed on a flat surface, it will rest on the anterior and posterior ends with gaps on either side. Abalones rotate their shells up to 180° many times each day, grinding down the irregularities of the shell margin relative to the substrate. Thus, when transplanted to flat abrasive surfaces, such as the tiles used in these experiments, this behavior will abrade away the

anterior and posterior ends. Whites have a much thinner shell than either pinks or greens, so that whites that had grown on a convex substrate would probably lose material from the anterior margin of the shell more rapidly and to a greater extent than either greens or pinks. In nature, the latter two species live mainly in cracks and crevices on flat surfaces, so the margin of their shell aperture tends to lie in a plane. Thus, pinks and greens placed on tiles will not wear away the anterior shell margin in the same manner as do whites. This loss in whites did not happen in the laboratory experiments, since the aquaria were made of acrylic or polyethylene plastic, both of which are softer than abalone shell.

Growth in Weight

Changes in body weight may or may not parallel those in shell length. To investigate growth in weight, we constructed a relationship between the logarithms of wet soft-body weight (without shell) and shell length, using measurements from large numbers of animals collected for reproductive assays. These variables are very highly correlated for each of the three species, as shown in Table 8. Using these equations the growth in weight for each species was calculated. As indicated by TUTSCHULTE (1976), the observed rates and the von Bertalanffy curves of relative weight change show that the rate of relative weight increase is highest for the smallest individuals and declines gradually with size. There is no abrupt discontinuity in the rate of decline at sexual maturity, which occurs at age 3 to 4 yr in pinks, 4 to 5 yr in whites and 6 yr in greens (TUTSCHULTE & CONNELL, 1981).

DISCUSSION

Our direct observations of growth rates for marked pink and green abalones agree closely for all treatments within species at the shallower depths and in the laboratory. When these species were transplanted to greater depths, and when large white abalones were transplanted from natural convex substrates to hard artificial ones, rates were lower. Since the former rates agreed among treatments and were similar to those based upon polymodal size-frequency analyses, we are inclined to accept them as reasonable estimates of growth of these three species at Santa Catalina Island.

The approximately linear juvenile growth rates described here for pink, green, and white abalones are similar to those reported for *Haliotis discus hannai* Ino (SAKAI, 1962), *H. tuberculata* L. (FORSTER, 1967), *H. midae* L. (NEWMAN, 1968), *H. rufescens* Swainson (LEIGHTON, 1968), *H. iris* Martyn (POORE, 1972), and *H. laevigata* Donovan (SHEPHERD & HEARN, 1983). Growth rates apparently slow down after age 3 to 5 yr.

The maximum lengths of these abalones range from about 100 mm for *Haliotis tuberculata* (FORSTER, 1967) to more than 280 mm for *H. rufescens* (COX, 1962). The largest individuals that we collected were much smaller

Table 5

Seasonal variations in shell growth rates of abalones held in the field in cages at two depths.

	Late summer/ autumn	Early winter	Late winter/ spring	Spring/ summer	Late summer/ autumn	Early winter
	Inclusive dates					
	24/VII/70 to 16/X/70 84	16/X/70 to 8/I/71 84	8/I/71 to 14/IV/71 96	14/IV/71 to 23/VII/71 100	23/VII/71 to 11/XI/71 111	20/XI/70 to 20/II/71 92
Interval (days)						
	Pinks (9 m depth)					Pinks (2 m depth)
<i>n</i>	15	25	25	25	25	24
Mean initial length (mm)	37.7	39.2	40.8	43.7	49.4	37.8
Mean growth rate (mm/100 days)	2.11	2.02	3.08	5.70	1.44	2.20
	Greens (9 m depth)					Greens (2 m depth)
<i>n</i>	4	5	5	5	5	19
Mean initial length (mm)	39.5	33.3	34.2	35.1	39.9	39.8
Mean growth rate (mm/100 days)	6.13	1.43	0.94	4.80	5.77	1.50

than the 254-mm (10-inch) maximum that COX (1962) listed for these three abalones. The asymptotic sizes we calculated (Table 3) were, in all but one case, quite similar to the largest individuals we collected.

The annual growth rates we report here for pink, green, and white abalones fall within the range of growth rates reported for other abalone species of similar maximum sizes with the exception of that of SHEPHERD & HEARN (1983). All but one of the abalone growth studies we have cited report annual rates of 15 to 30 mm for the first few years, followed by a progressive decline in annual growth rates. Only SHEPHERD & HEARN (1983) report significantly faster growth rates: first year growth of 40 to 50 mm followed by 32 and 29 mm in the second and third years for *Haliotis laevigata*.

The uniquely high rate of growth in the first year reported by SHEPHERD & HEARN (1983) was estimated by projecting the mean weekly growth rate of 0.9 mm for a group of 14- to 20-mm juveniles back to settlement. Thus, they estimated abalones 10 mm long to be about 11 weeks old. However, detailed measurements of young abalones indicate that their growth curve continually accelerates during early life. For example, POORE (1972) with *Haliotis iris* and SHEPHERD *et al.* (1985) with *H. scalaris* Leach found such a pattern. Likewise, white abalones reared in the laboratory by LEIGHTON (1972, 1974) averaged 13.4 mm at the age of 1 yr, whereas we found laboratory growth of 1- to 3-year-olds of 25.1 mm/yr. Thus, the abalones measured by SHEPHERD & HEARN (1983) were probably still in the phase of accelerating growth rate when measured. If so, a linear extrapolation back to settlement would underestimate age and thus overestimate average growth rate. Whether the unusually high growth rates of SHEP-

HERD & HEARN (1983) indicate true rates, or possibly are overestimates, requires further investigation.

Good evidence exists (*e.g.*, CRISP & PATEL, 1961; LECREN, 1962; MURDOCH, 1966) for the claim that the cost of reproduction may reduce growth and survival of some organisms. Thus, the generalization that the processes of growth, maintenance, and reproduction compete for the organism's limited energy resources (CONNELL & ORIAS, 1964; GADGIL & BOSSERT, 1970) may apply to abalones. TUTSCHULTE (1976) showed that both the total amount of gonadal material produced each year and its ratio to body-weight increment steadily increased following sexual maturity.

The hypothesis that a shift in energy allocation into reproduction causes a reduction in growth is supported by some but not all of the evidence in this study. Growth does

Table 6

Analysis of variance of seasonal growth of abalones shown in Table 5, using the data for the last four seasons at 9 m depth.

Source	df	Mean square	F	P
1. Pink abalones				
Seasons	3	90.30	30.00	0.0001
Individuals	24	5.67	1.88	>0.10
Error	72			
2. Green abalones				
Seasons	3	36.71	11.21	0.02
Individuals	4	13.43	4.10	0.10
Error	12			

Table 7

Seasonal variation in growth rates of abalones held in the laboratory. Values are the increment/100 days, given as the mean/SD (n).

Season	Pinks		Whites		Greens: immature, <100 mm
	Immature, <50 mm	Mature, \geq 50 mm	Immature, <100 mm	Mature, \geq 100 mm	
Winter/spring: 20 Dec 72-18 June 73	—	4.72/1.87 (3)	17.50/1.13 (3)	5.68/3.65 (4)	7.06/1.73 (2)
Spring: 10 March-18 June 73	8.67/1.44 (14)	6.80/1.13 (2)	—	—	—
Summer: 18 June-2 Oct 73	7.06/1.48 (12) **	5.57/1.57 (5) **	8.16/1.67 (2)	5.43/0.50 (3)	2.88/0.06 (2)
Autumn: 2 Oct 73-2 Jan 74	3.87/1.67 (11) ns	1.60/1.53 (6) **	3.07/0.06 (3)	0.45/0.79 (6)	4.80/2.16 (16)
Winter: 2 Jan-11 Apr 74	3.25/1.89 (10)	3.03/2.70 (6)	4.13/1.12 (3)	2.57/1.90 (3)	5.48/1.69 (16)

Comparisons of growth rates of individual pink abalones between certain pairs of seasons were made using the Wilcoxon matched-pairs signed ranks test. The results are indicated as ** $0.01 > P > 0.001$ and ns = $P > 0.05$.

slow down in older abalones, but not abruptly at the age of sexual maturity (Figures 1-3). However, as shown in Table 7, the growth of adult pink abalone was significantly less in the autumn, when gonads rapidly enlarge, than in the preceding summer or following winter. Since the juveniles also decrease in growth from summer to autumn, this seasonal reduction could be explained by reductions in temperature or by unknown other environmental changes. However, the fact that the growth of adults then increases in winter, whereas that of juveniles remains low, suggests that, once gonads have ceased enlarging in the late autumn, energy is again allocated to shell and somatic body growth in adults.

FORSTER (1967) stated that the size at which growth decreased coincided with that of sexual maturity in *Haliotis tuberculata*. PAUL *et al.* (1977) found that sexually mature *H. kamtschatkana* Jones held in the laboratory did not grow during the 90 days preceding spawning, then grew rapidly during the following 90 days. SHEPHERD & HEARN (1983)

reported that for both *H. laevigata* and *H. ruber* Leach, in a location where sea temperature varies little and the food supply seems abundant all year, the period of gonad production coincides with a lower growth rate. In summary, some analyses of seasonal variations in growth and gonad production in abalones support the hypothesis that the cost of reproduction reduces growth.

ACKNOWLEDGMENTS

We wish to thank the many people who helped with the diving involved in the field work for this study. We also thank Peter Frank and another reviewer for their careful comments on the paper. Stephen Schroeter assisted with the statistical analyses. We are also indebted to the staff of the Santa Catalina Marine Biology Laboratory of the University of Southern California for their hospitality in providing laboratory space and equipment.

LITERATURE CITED

- BERTALANFFY, L. VON. 1934. Untersuchungen über die Gesetzlichkeit des Wachstums. 1. Arch. Entwicklunsgmech. Organ. 131:613.
- BERTALANFFY, L. VON. 1938. A quantitative theory of organic growth (inquiries on growth laws. 11). Human Biology 10: 181-213.
- BERTALANFFY, L. VON. 1960. Principles and theory of growth. Pp. 137-359. In: W. W. Nowinski (ed.), Fundamental aspects of normal and malignant growth. Elsevier: Amsterdam.
- BEVERTON, R. H. J. 1954. Notes on the use of theoretical models in the study of the dynamics of exploited fish populations. U.S. Fish. Lab., Beaufort, North Carolina, Misc. Contrib. 2:159.

Table 8

Weight-length relationships of pink, green, and white abalones. Regression of wet soft-body weight in grams on shell length in mm, using natural logarithms for both length and weight.

Species	n	Slope	Intercept	r	P
Pink	100	3.23	-10.46	0.996	≤ 0.01
Green	86	3.38	-11.12	0.996	≤ 0.01
White	109	4.02	-14.51	0.929	≤ 0.01

- BEVERTON, R. H. J. & S. J. HOLT. 1957. On the dynamics of exploited fish populations. Great Brit. Min. Agr. Fish., Fish. Invest., Ser. 2, 19:1-533.
- BRODY, S. 1927. Growth rates. Univ. Missouri Agric. Exp. Sta. Bull. 97.
- CASSIE, R. M. 1950. The analysis of polymodal frequency distributions by the probability paper method. N.Z. Sci. Rev. 8:89-91.
- CASSIE, R. M. 1954. Some uses of probability paper in the analysis of size frequency distributions. Austral. Jour. Mar. Freshwater Res. 5:513-533.
- CONNELL, J. H. & E. ORIAS. 1964. The ecological regulation of species diversity. Amer. Natur. 98:399-414.
- COX, K. W. 1962. California abalones, family Haliotidae. Fish Bull., California, No. 118.
- CRISP, D. J. & B. PATEL. 1961. The interaction between breeding and growth rate in the barnacle *Elminius modestus* Darwin. Limnol. Oceanogr. 6:105-115.
- CROFTS, D. R. 1929. *Haliotis*. Liverpool Mar. Biol. Comm., Mem. No. 29.
- EBERT, T. A. 1973. Estimating growth and mortality rates from size data. Oecologia 11:281-298.
- EBERT, T. A. 1975. Growth and mortality of post-larval echinoids. Amer. Zool. 15:755-775.
- EBERT, T. A. 1980. Estimating parameters in a flexible growth equation, the Richards function. Can. Jour. Fish. Aquat. Sci. 37:687-692.
- FABENS, A. J. 1965. Properties and fitting of the von Bertalanffy growth curve. Growth 29:265-289.
- FORD, E. 1933. An account of the herring investigations conducted at Plymouth during the years from 1924-1933. Jour. Mar. Biol. Assoc. U.K. 19:305-384.
- FORSTER, G. R. 1967. The growth of *Haliotis tuberculata*: results of tagging experiments in Guernsey 1963-65. Jour. Mar. Biol. Assoc. U.K. 47:287-300.
- FOURNIER, D. A. & P. A. BREEN. 1983. Estimation of abalone mortality rates with growth analysis. Trans. Amer. Fish. Soc. 112:403-411.
- GADGIL, M. & W. H. BOSSERT. 1970. Life historical consequences of natural selection. Amer. Natur. 104:1-24.
- GREEN, R. H. 1970. Graphical estimates of rates of mortality and growth. Jour. Fish. Res. Bd. Can. 27:204-208.
- HARDING, J. P. 1949. The use of probability paper for the graphical analysis of polymodal frequency distributions. Jour. Mar. Biol. Assoc. U.K. 28:141-153.
- HASSELBLAD, V. 1966. Estimation of parameters for a mixture of normal distributions. Technometrics 8:431-444.
- HAYASHI, I. 1980. Structure and growth of a shore population of the ormer, *Haliotis tuberculata*. Jour. Mar. Biol. Assoc. U.K. 60:431-437.
- LECREN, E. D. 1962. The efficiency of reproduction and recruitment in freshwater fishes. Pp. 283-296. In: E. D. LeCren & M. W. Holgate (eds.), The exploitation of natural animal populations. Blackwell: Oxford.
- LEIGHTON, D. L. 1968. A comparative study of food selection and nutrition in the abalone, *Haliotis rufescens* (Swainson) and the sea urchin, *Strongylocentrotus purpuratus* (Stimpson). Ph.D. Dissertation, University of California, San Diego.
- LEIGHTON, D. L. 1972. Laboratory observations on the early growth of the abalone, *Haliotis sorenseni*, and the effect of temperature on larval development and settling success. Fish. Bull. 70:373-381.
- LEIGHTON, D. L. 1974. The influence of temperature on larval and juvenile growth in three species of southern California abalones. Fish. Bull. 72:1137-1145.
- MACDONALD, P. D. M. & T. J. PITCHER. 1979. Age-groups from size-frequency data: a versatile and efficient method for analyzing distribution mixtures. Jour. Fish. Res. Board Can. 36:987-1001.
- MCMNEW, R. W. & R. C. SUMMERFELT. 1978. Evaluation of a maximum-likelihood estimator for analysis of length-frequency distributions. Trans. Amer. Fish. Soc. 107:730-736.
- MURDOCH, W. W. 1966. Population stability and life history phenomena. Amer. Natur. 100:5-11.
- NEWMAN, G. G. 1968. Growth of the South African abalone, *Haliotis midae*. Div. Sea Fish. S. Afr., Invest. Rep. No. 67.
- PAUL, A. J., J. M. PAUL, D. W. HOOD & R. A. NEVE. 1977. Observations on food preferences, daily ration requirements and growth of *Haliotis kamtschatkana* Jonas in captivity. Veliger 19:303-309.
- POORE, G. C. B. 1972. Ecology of New Zealand abalones, *Haliotis* species (Mollusca: Gastropoda) 3. Growth. N.Z. Jour. Mar. Freshwater Res. 6:534-559.
- RICKER, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Fish. Res. Bd. Can. Bull. 191:382 pp.
- SAINSBURY, K. J. 1980. Effect of individual variability on the von Bertalanffy growth equation. Can. Jour. Fish. Aquat. Sci. 37:241-247.
- SAINSBURY, K. J. 1982. Population dynamics and fishery management of the paua, *Haliotis iris* 1. Population structure, growth, reproduction and mortality. N.Z. Jour. Mar. Freshwater Res. 16:147-161.
- SAKAI, S. 1962. Ecological studies on the abalone, *Haliotis discus hannai* Ino IV. Studies on the growth. Bull. Jap. Soc. Sci. Fish. 28:899-904.
- SCHNUTE, J. & D. FOURNIER. 1980. A new approach to length-frequency analysis: growth structure. Can. Jour. Fish. Aquat. Sci. 37:1337-1351.
- SHEPHERD, S. A., P. S. CLARKSON & J. A. TURNER. 1985. Studies on southern Australian abalone (genus *Haliotis*). V. Spawning, settlement and early growth of *H. scalaris*. Trans. Royal Soc. S. Austr. 109:61-62.
- SHEPHERD, S. A. & W. S. HEARN. 1983. Studies on southern Australian abalone (genus *Haliotis*). IV. Growth of *H. laevigata* and *H. ruber*. Austr. Jour. Mar. Freshwater Res. 34:461-475.
- TUTSCHULTE, T. C. 1976. The comparative ecology of three sympatric abalones. Ph.D. Dissertation, University of California, San Diego.
- TUTSCHULTE, T. C. & J. H. CONNELL. 1981. Reproductive biology of three species of abalone (*Haliotis*) in southern California. Veliger 23:195-206.
- TUTSCHULTE, T. C. & J. H. CONNELL. In press. Feeding behavior and the distribution, abundance and productivity of algal food of three species of abalones (*Haliotis*) in southern California. Mar. Ecol. Prog. Ser.
- WALFORD, L. A. 1946. A new graphic method of describing the growth of animals. Biol. Bull. 90:141-147.
- YONG, M. Y. Y. & R. A. SKILLMAN. 1975. A computer program for analysis of polymodal frequency distributions (ENORMSEP), FORTRAN IV. Fish. Bull. 73:681.